A New Multituberculate from the Late Cretaceous Locality Ukhaa Tolgod, Mongolia. Considerations on Multituberculate Interrelationships*

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ABSTRACT

Tombaatar sabuli, a new taxon from the recently discovered Upper Cretaceous locality of Ukhaa Tolgod, Mongolia is a large multituberculate, similar to *Catopsbaatar catopsaloides* and *Djadochtatherium matthewi*. A preliminary cladistic analysis employing a modified version of Simmons' (1993) matrix, of 67 characters and 50 taxa, yielded 20,000 equally most parsimonious trees before exhausting the available computer memory. The large amount of missing data (10 taxa are less than 25% complete) probably accounts for the high number of trees and the relatively poor resolution of the strict consensus tree. A monophyletic group formed by *Tombaatar*, and *Catopsbaatar*, with *Djadochtatherium*, *Nemegtbaatar*, *Bulganbaatar*, *Kryptobaatar* and *Chulsanbaatar*, as successive sister groups is support-ed in the strict consensus tree of this heuristic run. The remaining Late Cretaceous multituberculates from Mongolia and *Pentacosmodon* (Paleocene of North America) join this group in the 50% majority rule consensus tree. In all cases, this group falls outside Cimolodonta (ptilodontoids + taeniolabidoids). The topologies of the recovered trees suggest that most of the Late Cretaceous Mongolian multituberculates form an endemic monophyletic group. This idea, however, has to be considered provisional until a full review of multituberculate relationships is completed. Most multituberculates, including *Tombaatar*, have a notably large maxillary sinus, nasal cavity, and olfactory lobes. The peculiar shape of the multituberculate rostrum reflects the unique morphology of their nasal region.

INTRODUCTION

Fossil remains of multituberculates range in age from probably Late Triassic (Hahn et al., 1987) to Late Eocene (Kristhalka et al., 1982; Prothero and Swisher, 1992) and their durable teeth and jaws are known from all major landmasses with the exception of Australia and Antarctica. Despite the wide temporal and geographical range of this group, most taxa are known by isolated teeth and fragmentary upper and lower jaws. Multituberculates are the most abundant and diverse mammal fossils from the continental Late Cretaceous Formations of Mongolia (Kielan-Jaworowska, 1974; Dashzeveg et al., 1995) and they are frequently represented by nearly complete skulls. Because of the high quality and abundance of specimens, the Mongolian multituberculates are central to our understanding of the morphology and relationships of this group (Kielan-Jaworowska, 1970, 1974; Kielan-Jaworowska et al., 1986; Gambaryan and Kielan-Jaworowska, 1995). The new, extraordinarily large sample of multituberculate skulls collected in the last five years by the Mongolian Academy of Sciences–American Museum expeditions, in addition to significant collections previously amassed by Mongolian, Russian and Polish expeditions, will allow a comprehensive assessment of the group. Mongolian multituberculates have been collected in traditional areas made famous by dinosaurs remains, such as the Flaming Cliffs (Andrews, 1932; Kielan-Jaworowska and Barsbold, 1972), or in newly found localities, such as Ukhaa Tolgod (Dashzeveg et al., 1995) which has yielded an unparalleled concentration of mammals, dinosaurs, and other vertebrates.

Some Mongolian multituberculates (*Kryptobaatar* and *Chulsanbaatar* among others) are known from scores of skulls and occasionally by associated postcrania (Simpson, 1928; Kielan-Jaworowska, 1969, 1979; Kielan-Jaworowska and Gambaryan, 1994; Dashzeveg et al., 1995). Two taxa of relatively large size, *Djadochtatherium matthewi* (Simpson, 1925) and *Catopsbaatar catopsaloides* (Kielan-Jaworowska, 1994; = *Djadochtatherium catopsaloides* Kielan-Jaworowska, 1974) are less abundant in Mongolian collections. The former is known only

by the type specimen, an incomplete skeleton (Simpson, 1925, 1928), and the latter is represented by three skulls and several lower jaws, plus a few postcranial elements. The specimen we describe in this paper represents a new taxon; it is of large size for the average dimensions of most Mongolian multituberculates, but similar to those previously mentioned and probably closely related to them. The systematic assignments of both *Djadochtatherium* and *Catopsbaatar* have varied considerably. *Catopsbaatar catopsaloides* (Kielan-Jaworowska, 1994) has been attributed successively to *Djadochtatherium*, *Catopsalis*, and finally to a genus of its own (Kielan-Jaworowska, 1974, 1994; Kielan-Jaworowska and Sloan, 1979). On the other hand, *Djadochtatherium matthewi* was at one time transferred to *Catopsalis* (Kielan-Jaworowska and Sloan, 1979), but later returned to the original genus (Simmons and Miao, 1986). The new material warrants the reevaluation of these taxa based in a preliminary cladistic analysis.

MATERIAL AND LOCALITY

The type and only known specimen of the new taxon we describe here, a partial skull (PSS-MAE 122), was collected in Ukhaa Tolgod, Nemegt Basin, Gobi desert (Dashzeveg et al., 1995) during the 1993 field season by members of the Mongolian Academy of Sciences–American Museum of Natural History expedition. Nevertheless, there are several skulls that likely represent the same taxon among the numerous—still only partially prepared—specimens from Ukhaa Tolgod. A large sample of complete skulls of *Kryptobaatar* have also been recovered (Novacek et al., in prep.) from the same part of the sequence of Ukhaa Tolgod.

Ukhaa Tolgod is a small amphitheater in the eastern Nemegt Valley about 300 km southwest of the famous Flaming Cliffs, or Bayn Dzak, locality (see Dashzeveg et al., 1995). The terrain consists of low hills, buttes, cliffs, and broad flat slopes that surround a shallow wash. The primary collecting area is only about 4 km^2, but some 20 sublocalities have been found and mapped within that area. These sites together account

for an unprecedented wealth of high-quality specimens representing a diversity of Mesozoic vertebrate groups—-including over 150 skeletons of theropod, protoceratopsian, and ankylosaurian dinosaurs; 240 and 300 skulls (many with skeletons) of mammals and lizards, respectively; numerous nests with dinosaur eggs; embryonic, juvenile, and adult theropods associated with nests; and several skeletons of the flightless bird *Mononykus* (Perle et al., 1994; Norell et al. 1994, 1995; Dashzeveg et al., 1995; Novacek et al., 1996).

The section at Ukhaa Tolgod bears a striking resemblance to the type section of the Djadokhta Formation at Bayn Dzak (Dashzeveg et al., 1995; Dingus et al., in prep.). It comprises a basal section of red sandstone with concretionary sheets; a middle section of thick cross-bedded units of cliff-forming red sandstones; and an uppermost fluvial sequence of interbedded red sandstones, brown and maroon mudstones, and conglomerates. Fossils occur throughout the section but the highest concentrations of vertebrates are in the basal and middle sandstones. It is noteworthy that multituberculate and lizard fossils are common, but larger skeletons of dinosaurs are rare in the upper fluvial sequence. Many skeletons at Ukhaa Tolgod are articulated and nearly complete and show little surface pitting or destruction. It is suggested that the preserved animals were rapidly buried in sand soon after or even at the time of death, but the taphonomic factors bearing on this case are under investigation (Dashzeveg et al., 1995; Novacek et al., in prep.). A similar scenario has been suggested for the Djadokhta-like strata at Bayan Mandahu in northern China (Jerzykiewicz et al., 1993).

METHODS

We included the new taxon and employed the matrix presented by Simmons (1993) as a source for characters and taxa in the cladistic analysis. Character coding for *Kryptobaatar* was revised based on recently collected skulls from Ukhaa Tolgod (PSS-MAE 101) and Tugrugeen Shireh (PSS-MAE 113). Character coding for *Djadochtatherium matthewi*, *Catopsbaatar catopsaloides*, and *Ne-*

megtbaatar gobiensis was altered to reflect our reinterpretation of the available specimens. The purpose of this analysis is not to present an extensive survey of the relationships of all the major taxa of multituberculates, but to offer a preliminary hypothesis of the relationships of the new taxon. Thus, with few exceptions, the coding has been taken directly from Simmons study for those taxa not mentioned above. The exceptions pertain to changes suggested by Dr. Zofia Kielan-Jaworowska when she reviewed an earlier version of this paper.

Many of the 50 taxa included have a very low percentage of completeness: 10 of them are 25% complete or less, and 23 are below 50%. The proliferation of trees resulting from the numerous missing data is likely to obscure the underlying hierarchical structure present in the most parsimonious trees when a consensus tree is computed (Swofford, 1991; Novacek, 1992). To cope with the effects of the missing data, Taxonomic Equivalent Taxa (TET) were identified following the rules proposed by Wilkinson (1995) for consistent taxonomic reduction. Four TET were removed from the original matrix: *Guimarotodon*, *Mesodma*, *Mimetodon*, and *Baiotomeus*; they are TET of the more complete taxa *Ctenacodon*, *Paraectypodus*, *Neoplagiaulax*, and *Ptilodus* respectively. Two pairs, *Mimetodon-Neoplagiaulax* and *Baiotomeus-Ptilodus*, did not fully meet the second rule of Wilkinson (1995), because, in both cases, the less complete member of each pair had one character coded as polymorphic (uncertainty), while the more complete taxon, or index, had only one of the two possible states. When the polymorphic condition was changed to conflict with that of the index taxon, the topology of the consensus tree did not change. Thus, the taxonomic difference between these taxa, if any, appeared to be minimal. Operationally, we assumed that *Mimetodon* and *Baiotomeus* are TET of *Neoplagiaulax* and *Ptilodus* respectively. Taxa deleted from the original analysis were *a posteriori* placed manually in the consensus trees in a trichotomy between the index taxon and its sister group (fig. 6B). This was possible because in each case the TET were equivalent to only one of the index taxa and consequently their position in the tree was

unequivocally determined by the index taxon (Wilkinson, 1995).

Tugrigbaatar, from Tugrugeen Shireh, originally included in Simmons (1993) study is considered by us to be a junior synonym of *Kryptobaatar* and consequently is removed from our matrix (see below). The multistate characters considered as ordered by Simmons were treated in the same way here. The matrix was subjected to analysis by PAUP 3.1.1 (Swofford, 1993), and polymorphism was treated as uncertainty.

The anatomical nomenclature follows in most cases Kielan-Jaworowska (1971), Kielan-Jaworowska et al. (1986), Miao (1988), Hurum (1994), and Gambaryan and Kielan-Jaworowska (1995). The systematic terminology follows Simmons (1993), whenever possible, but more traditional terms are also applied.

Institutional abbreviations are as follow: AMNH, American Museum of Natural History, Vertebrate Paleontology; PSS-MAE, Paleontological and Stratigraphic Section (PSS) of the Geological Institute, Mongolian Academy of Sciences, Ulaan Baatar, Mongolia, and collections of the joint Mongolian Academy of Sciences—American Museum of Natural History Paleontological Expeditions (MAE); ZPAL, Institute of Paleobiology of the Polish Academy of Sciences, Warsaw.

SYSTEMATICS

CLASS MAMMALIA

SUBCLASS ALLOTHERIA

INFRACLASS MULTITUBERCULATA

FAMILY INCERTAE SEDIS

Tombaatar, new genus (figs. 1–5)

TYPE AND ONLY SPECIES: *Tombaatar sabuli*, new species.

ETYMOLOGY: *Tom*, transliteration from the Mongolian, big; and *baatar*, transliteration from the Mongolian for hero, a common suffix for Mongolian multituberculates. *sabuli*, Latin, from the sand, referring to the sand dunes and related terrain of the Gobi desert at present and also when *Tombaatar* lived during the Late Cretaceous.

HOLOTYPE: PSS-MAE 122, a partial skull with fragmentary rostrum and anterior portion of the braincase, with both I2, right I3, left P1, P3, and left and right P4, M1-2.

LOCALITY: Ukhaa Tolgod, unnamed formation (Djadokhta Formation equivalent?), Upper Cretaceous (see also above).

DIAGNOSIS: Large size multituberculate, with palate length (measured from the posterior margin of the I2) of 30.4 mm and a M1-M2 length of 9.5 mm. Palatal torus is notably strong, more than in any other presently known multituberculate, with an elaborated, stout, crescent-shaped process that projects ventrally on either palatine (as in the weaker torus of *Kryptobaatar*). M1 cusp formula (4:5:2) and size, differentiate *Tombaatar* from all Mongolian multituberculates. Skull of *Tombaatar* is similar in dimensions to those of *Djadochtatherium matthewi* (Simpson, 1925) and *Catopsbaatar catopsaloides* (Kielan-Jaworowska, 1974, 1994; Kielan-Jaworowska and Sloan, 1979), but differs from these taxa in having the I3 alveolus formed by both the premaxilla and maxilla; a slender, posteriorly tapering process of the premaxilla on the rostrum; a high skull with a deep orbit (flat rostrum, and palate wider and shorter in *Djadochtatherium* and *Catopsbaatar*); and a proportionately short and slender anterior process of the frontal on the skull roof (long and wide in *Djadochtatherium*, but not preserved in *Catopsbaatar*). P2 absent and rounded premaxillary-maxillary suture in rostrum of *Tombaatar* and *Catopsbaatar* (P2 present and suture not rounded in *Djadochtatherium*; suture rounded in *Nemegtbaatar*, *Kryptobaatar*, and *Chulsanbaatar*, but not in *Sloanbaatar*, *Kamptobaatar*, *Ectypodus*, or *Lambdopsalis*). *Tombaatar* and *Djadochtatherium* are distinguished from *Catopsbaatar* in having large P1 and P3 (?plesiomorphic) and M1 with only two cusps on the lingual row which form a lobe in the posterior half of the molar of *Tombaatar*. Four lingual cusps cover the posterior two-thirds of the labial margin of the M1 in *Catopsbaatar*. Some additional characters are present in other multituberculates but are rendered autapomorphies of *Tombaatar* by their distribution on the most parsimonious trees. These are: base of zygomatic arch dorsal or anterior to P3/P4 embrasure, incisive foramina of medium size and elongated, and
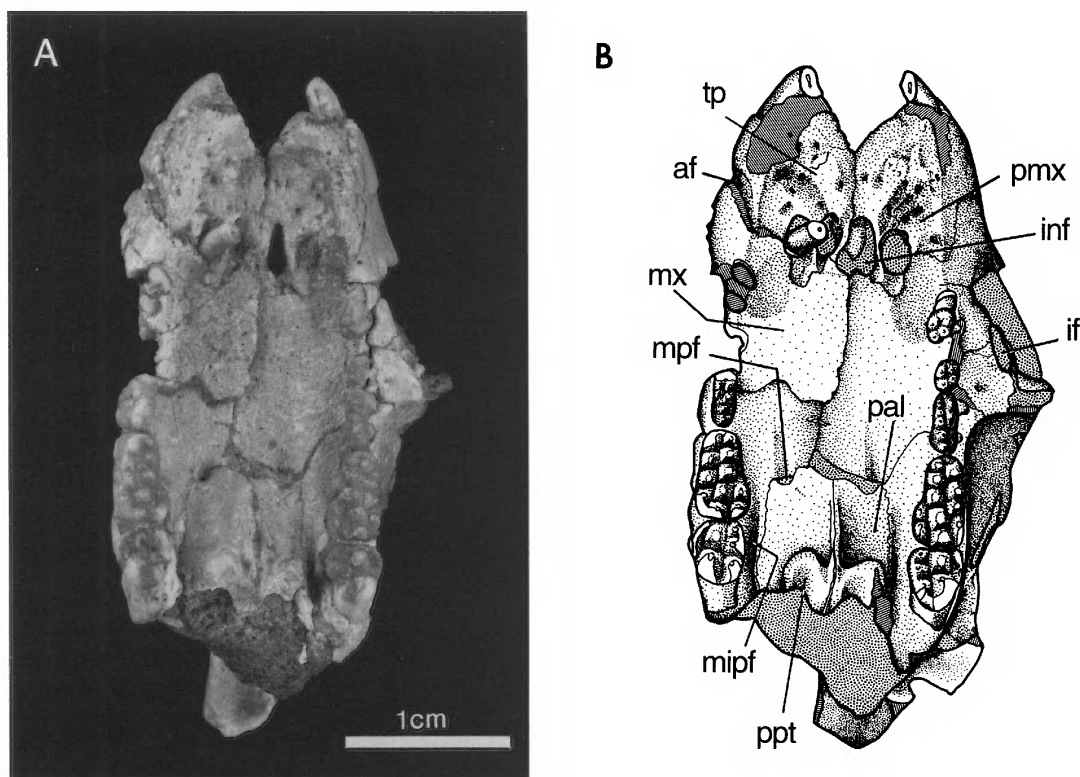
Fig. 1.   Photograph (**A**) and drawing (**B**) of the type specimen of *Tombaatar sabuli* PSS-MAE 122 in ventral view. Abbreviations: af, articular facet for the maxilla; if, infraorbital foramen; inf, incisive foramina; mpf, major palatine foramen; mipf; minor palatine foramen; mx, maxilla; pal, palatine; pmx, premaxilla; ppt, postpalatine torus; tp, thickening of premaxilla.

posterior margin of palate medial to middle of M2.

DESCRIPTION

Skull

Figures 1–3

The type and only specimen, PSS-MAE 122, is a fragmentary rostrum and anterior portion of the braincase (figs. 1–3). The skull has a well preserved dentition, palate, and orbital wall, but most, or all, of the right premaxilla, maxilla, nasal, lacrimal, and frontal are not preserved. The partial loss of the wall of the nasal cavity has exposed the large maxillary sinus and infraorbital canal, allowing their preparation and description.

PREMAXILLA: For descriptive purposes, the premaxilla is composed of two processes, a fairly horizontal palatal process, or processus

palatinus, and a rather vertical nasal process, processus nasalis or facialis. The premaxilla constitutes the lateral and ventral wall of the anterior portion of the nasal cavity which is at the same time the roof of the oral cavity (figs. 1–3). This bone lodges the large I2, forms most of the alveolus for the I3, and articulates with the maxilla and the nasal.

In ventral view (fig. 1), the palatal process is incomplete anteriorly between the alveoli for I2. The preserved portion has an arched outline and is moderately concave dorsally. A blunt ventral ridge marks the labial margin of the palate, extending from the premaxilla-maxilla suture to the anteriormost extent of the premaxilla. Both premaxillae are in contact sagittally through a straight and smooth suture. The suture with the maxilla is more complex; it runs posteromedially from the labial margin until it reaches the caudal rim of
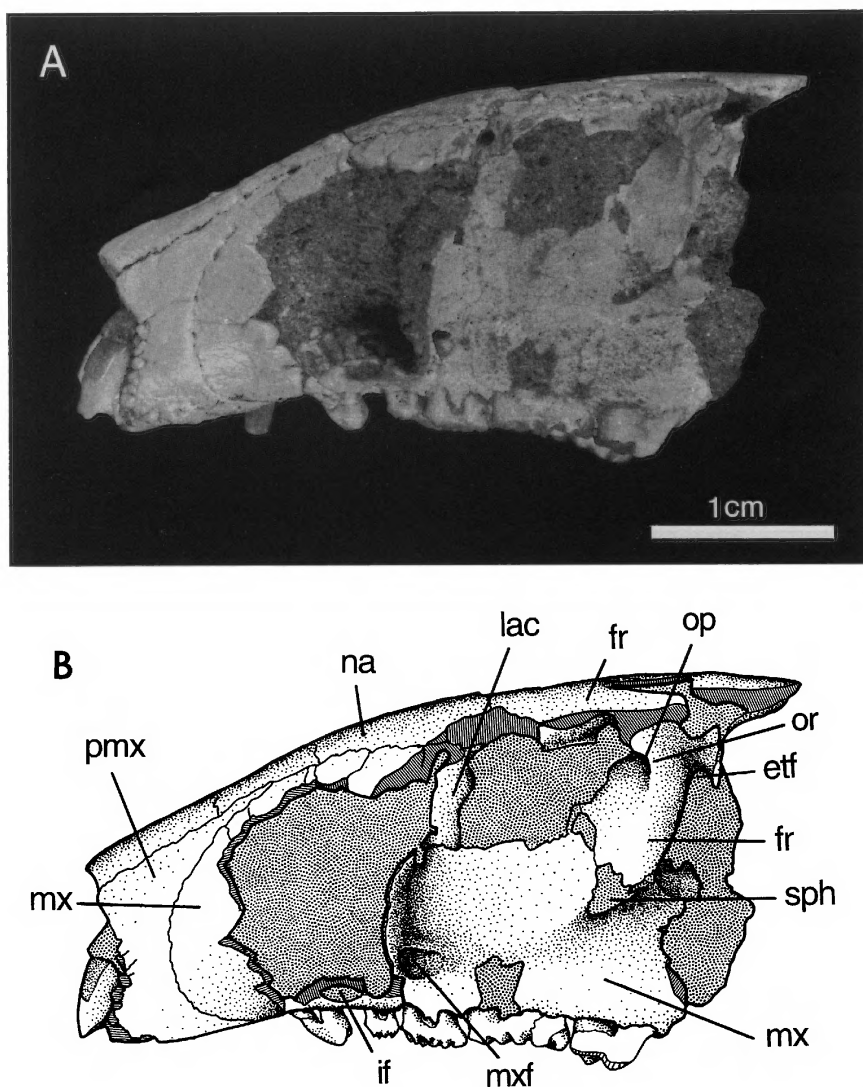
Fig. 2. Photograph (**A**) and drawing (**B**) of the type specimen of *Tombaatar sabuli* PSS-MAE 122 in lateral view. Abbreviations: etf, ethmoidal foramen; fr, frontal; if, infraorbital foramen; lac, lacrimal; mx, maxilla; mxf, maxillary foramen; na, nasal; op, orbital pocket; or, orbital ridge; pmx, premaxilla; sph, sphenopalatine foramen.

the alveolus for I3. At that point, the suture turns abruptly posteriorly and then antero-medially. The alveolus for I3 is circular and displaced medially from the labial margin, roughly in line with the I2 alveolus, a universal condition in the Late Cretaceous Mongolian multituberculates. The I3 alveolus is formed by both premaxilla and maxilla. A slender process of bone separates the I3 alveoli from the more medial incisive forami-na. The foramina are similar in size to the I3 alveoli, oval and medially bounded by stout palatine processes.

Rostral to the incisive foramen, the palatal process of the premaxilla displays a conspicuous boss, or raised area, similar to the structure present in *Kryptobaatar* and *Chulsanbaatar*. This is the thickening of the premaxilla of Kielan-Jaworowska et al. (1986). Several small foramina and pits are present on
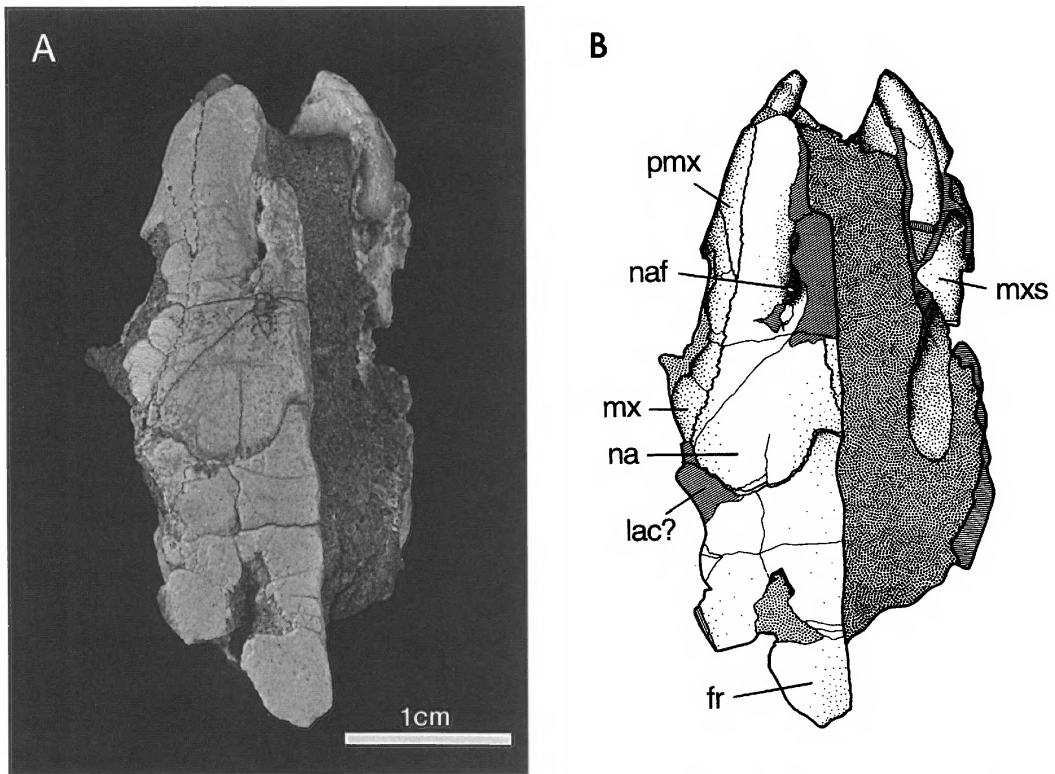
Fig. 3.   Photograph (**A**) and drawing (**B**) of the type specimen of *Tombaatar sabuli* PSS-MAE 122 in dorsal view. Abbreviations: fr, frontal; lac?, lacrimal?; na, nasal; naf, nasal foramen; mx, maxilla; mxs, maxillary sinus (floor); pmx, premaxilla.

the palatine process in front of incisive foramina. In lateral view, the alveolus for I2 is fully exposed on the right side by breakage of the alveolar wall; it extends back to the level of I3.

The nasal or facial process of the premaxilla (fig. 2) is extensive, very tall, and is in contact with the nasal and the maxilla exclusively; there is no evidence of a septomaxilla. The anterior margin of the nasal process is incomplete, exposing both I2 in their alveoli. The existence of an internarial process of the premaxilla, as occurs in *Lambdopsalis* (Miao, 1988), can neither be confirmed nor denied in *Tombaatar* due to poor preservation. The left premaxilla shows a faint indication of a depression running parallel to the labial margin. In some other better-preserved multituberculate skulls, like *Kryptobaatar* (PSS-MAE 101), a conspicuous groove parallel to the edge of the premaxilla is present.

The same structure is likely to have been present in *Tombaatar*.

The suture between the nasal and premaxilla is irregular with small interdigitating projections from both elements. The more damaged right side of the specimen reveals that the maxilla extensively overlaps the premaxilla laterally. The external contact between these two elements is a smooth rostrally convex suture preserved on the left side of the skull (fig. 2). A very long and slender posterior process of the premaxilla wedges between the maxilla and nasal, extending dorsally and posteriorly to the roof of the skull above P1.

MAXILLA: The maxilla is well developed in most multituberculates, being a primary component of the rostrum, zygomatic arch, and orbital mosaic. It has a horizontal palatal process, and subvertical facial and orbital processes. The maxilla contacts the premax-

illa anteriorly, with the nasal, frontal and probably lacrimal dorsally, and finally, with the palatine posteriorly in the palate. Only the contact with the frontal is preserved in the orbit. The maxilla also forms the dental arcade for P1, P3-4, and M1-2. The maxilla forms the posterior part of the nasal cavity, the anterodorsal portion of the cranial cavity, and the floor of the choanal passage. The zygomatic process and sizable portions of the facial and orbital process are missing. On the right maxilla, only the palatal process and portions of the facial process delimiting the maxillary sinus are preserved.

The palatal process of the maxilla (fig. 1) is broad, concave dorsally, and without palatal vacuities. Slightly compressed, the palatal processes of the maxillae are broken in four somewhat displaced pieces. The suture with the palatine has a transverse and a longitudinal section. The former is just posterior to the anterior margin of the M1 and it is notched near its most lateral point by the major palatine foramen for the nerve of the same name and accompanying vessels. A very faint groove continues anteriorly on the maxilla a short distance from the anterior edge of the major palatine foramen. The long longitudinal suture of the maxilla with the palatine limits medially a narrow process of the maxilla between the palatine and the molars. In this area, at the level of the M2 and very close to the maxilla-palatine suture, but completely encompassed by maxilla, is a slit-like foramen, the minor palatine foramen.

The extent of the maxilla posterior to the last molar cannot be ascertained because of breakage. However, in most Mongolian multituberculates the alisphenoid extends forward nearly to the palate. Therefore, it seems likely that not much of the maxilla in this region of PSS-MAE 122 is missing.

The facial process of the maxilla (fig. 2) shows a curved, serrated suture with the nasal. On the left side, the infraorbital canal opens anteriorly via the infraorbital foramen at the level above the small diastema between P1 and P3; the foramen is distinctively depressed dorsoventrally, a derived feature of some Mongolian multituberculates such as *Kryptobaatar*. A prominent shelf separates the medial rim of the foramen from the dental arcade. As preserved, the infraorbital ca-

nal lacks a roof and is confluent with the maxillary sinus. This, however, is likely an artifact of incomplete preservation.

The broken right maxilla has been prepared to expose the maxillary sinus (fig. 3). This sinus is notably large and seems to have been connected to the nasal cavity by a large fenestra. In the rostral part of the sinus, a thick anteroposterior crest that houses the root of the premolars protrudes dorsally and divides the sinus into medial and lateral cavities. The lateral cavity extends rostrally inside the process of the maxilla that overlaps the premaxilla laterally.

In lateral view (fig 2), the orbital process is exposed on the right and left side because of the absence of the zygomatic processes. The orbital process is a large bony lamina extending from the vicinity of the maxillary foramen anteriorly to the sphenorbital fissure posteriorly. The position of the latter fissure can only be approximated in this specimen. The circular posterior aperture of the infraorbital canal, the maxillary foramen, is enclosed by the base of the zygomatic process and the anterior portion of the orbital lamina. Consequently, as in all the previously described multituberculates from the Late Cretaceous of Mongolia, the infraorbital canal is formed entirely by the maxilla. In a poorly preserved area, inside the infraorbital canal and slightly anterior to the rim of the maxillary foramen, there is a deep notch directed medially toward the nasal cavity. This notch was probably a foramen when the bone was complete. The morphology of the area around the maxillary foramen resembles that of the specimen referred to *Djadochtatherium* by Gregory and Simpson (1926; see below).

Dorsally, the orbital lamina contacts the very incomplete orbital contribution of the lacrimal and possibly also the frontal, but the relevant portions of the latter bone are not preserved in the anterior part of the orbit. The posterior contact of the maxilla with the frontal runs obliquely ventroposteriorly in the orbit, ending at a point above M1-M2 in the probable region of the sphenopalatine foramen, where there is some damage. Most of the missing bone is probably maxilla, and the sphenopalatine foramen was placed between maxilla and frontal at the posterior edge of

this area. It is possible, although unlikely, that the orbitosphenoid formed a small portion of the caudal margin of the foramen. A broad sulcus continues posteromedially from the region of the sphenopalatine foramen in the direction of the region in which the sphenorbital fissure was present. The maxilla in this area is virtually a horizontal shelf that floors the sulcus.

PALATINE: According to Miao (1988), contrary to the condition present in most mammals, the multituberculate palatine is exposed only in the palate and it lacks an orbital process (Miao, 1988; contra Hurum, 1994). The palatine does not contribute to the orbital mosaic in *Tombaatar*. The nature of the suture with the maxilla already described gives this bone a subrectangular outline (fig. 1). The palatine is a horizontal lamina with medial and posterior ridges. The medial ridge, at the intrapalatine suture, forms a very sharp and raised crest which increases in relief posteriorly, where it meets the postpalatine torus. Massive and crescent-shaped, the postpalatine torus marks the posterior limit of the hard secondary palate with its strong ventral projection. The torus reaches ventrally almost to the level of the occlusal surface of M2. The bilateral arms of the torus meet at the midline to form a strong, blunt posterior process.

NASAL: As Simpson (1937) remarked, the nasal is very large in multituberculates. In *Tombaatar*, it is a long laminar bone which becomes broader and slightly lateromedially convex posteriorly. The nasal articulates with the premaxilla, maxilla, frontal, and probably also with the lacrimal.

The suture with the premaxilla (fig. 2, 3) is virtually parasagittal and irregular, but not serrated, as is the arched maxilla-nasal suture. Posteriorly (fig. 3), the nasal is overlapped in the midline by a short, wedge-shaped medial process of the frontal; lateral to this process, the suture is arch-shaped. Severe breakage of the bone in the region of the once-present orbital rim precludes an absolute identification of the relationships in this area. Nevertheless, the posterolateral sector of the nasal seems to be in contact with a separate, roughly rectangular bone. If this is correct, the bone in question can only be the lacrimal.

The anterior half of the nasal is narrow and perforated by two sizable nasal foramina anteroposteriorly aligned in a common sulcus.

LACRIMAL: A small, elongated fragment of bone contacting the orbital process of the maxilla is almost certainly part of the lacrimal (fig. 2). It seems to be continuous with the subrectangular element of the roof of the skull already mentioned in connection with the nasal (fig. 3, lac?). The lacrimal likely has both an orbital wing and a substantial exposure in the cranial roof, as is the case in other Mongolian multituberculates where this element is well preserved (Kielan-Jaworowska et al., 1986; Hurum, 1994).

FRONTAL: The limits of the frontal on the cranial roof and within the orbit have been described above; both the posterior and orbital margins of this bone are incomplete. The preserved portion of the orbital process of the frontal (fig. 2) is directed ventrally and is divided in two portions by a strong, vertical, orbital ridge (Gambaryan and Kielan-Jaworowska, 1995). In front of the ridge, and partially covered laterally by it, a deep pocket is found, the orbitonasal fossa (Kielan-Jaworowska et al., 1986) or orbital pocket (Gambaryan and Kielan-Jaworowska, 1995). In *Catopsbaatar* this anterolaterally trending ridge is continuous with the orbital margin and was likely so in *Tombaatar*, implying a large roof for the orbit as in all known late Cretaceous multituberculates from the Gobi. Behind the orbital crest, another depression, which is much broader and more open than the orbitonasal fossa, is directed toward a notch in the posterodorsal area of the frontal. The edges of this notch are natural, and the feature is here interpreted as the dorsal margin of the ethmoidal foramen, for the ethmoidal nerve (a branch of V_1) and vessels.

The frontal contribution to the cranial roof is slightly convex dorsally from front to back, and its posterior margin probably is close to representing the full length of this bone. No other characters can be described from this nearly featureless and broken surface (fig. 3).

Dentition
Figures 4, 5

The morphology of the dentition can be confidently interpreted despite some break-
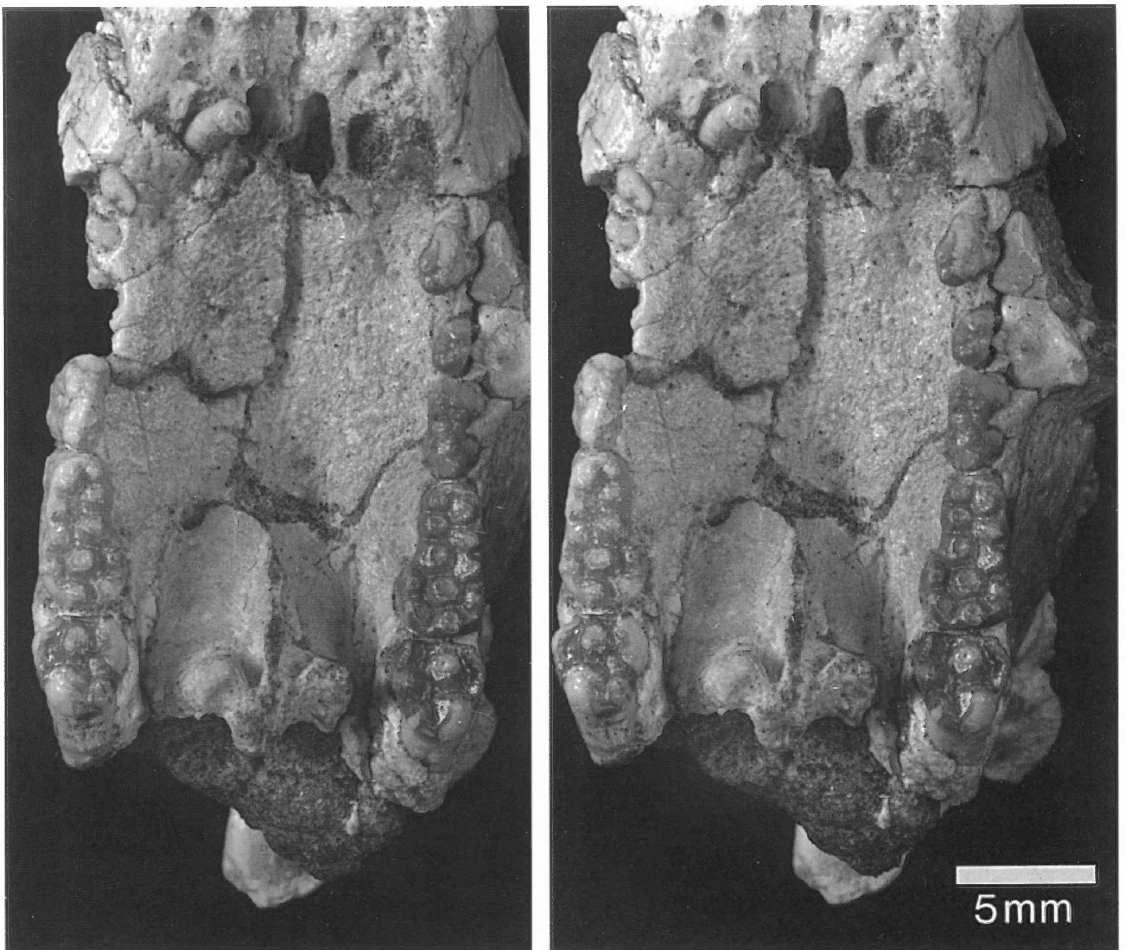
Fig. 4. Stereophotograph of the upper dentition of *Tombaatar sabuli* PSS-MAE 122 in occlusal view.

age or loss of some teeth. As a whole, the teeth do not show evidence of extensive wear, but distinctive facets crown each cusp. The formula of the upper dentition of *Tombaatar* is I2, C0, P3, M2.

INCISORS: As in cimolodontids, only I2 and I3 are present. I2 is broken on both sides at the level of the alveolus and the left I3 has been lost. I2 is a narrow and strong tooth with a long, curved root which extends posteriorly and dorsally inside the premaxilla to the contact of this bone with the maxilla. Part of the enamel preserved on the left I2 shows it was limited to a very thin band covering the anterolateral portion of the tooth.

I3 is a perfectly cylindrical tooth, slightly curved posteriorly and housed in an alveolus formed by the premaxilla and maxilla. This tooth is medially displaced from the margin of the premaxilla. There is no trace of enamel on I3, but this may be due to weathering, because the naturally exposed portions of I2 have also lost all traces of enamel, which is preserved on the surfaces of the tooth that was not exposed originally. I3 shows a flat surface with extensive wear, so that the original number of cusps cannot be ascertained.

PREMOLARS: *Tombaatar* has three premolars identified as P1, P3, and P4 respectively. Between the P1 and P3 there is a short diastema, shorter than P3, indicative of the expected position of the absent P2. P1 and P3 are known only in the left dentition.

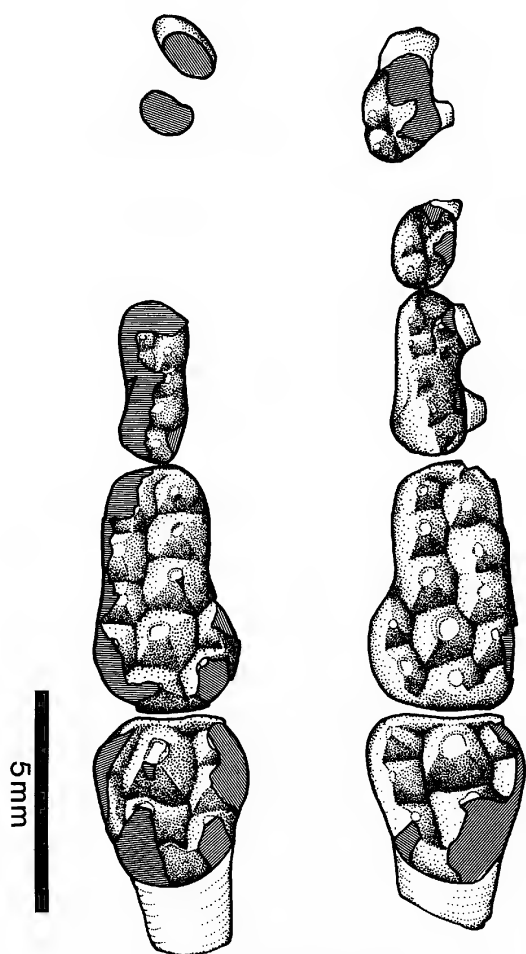P1 is doubled-rooted, with the anterior

Fig. 5.   Upper dentition of the type of *Tombaatar sabuli* PSS-MAE 122 in occlusal view. Cross hatching denotes missing enamel or broken surfaces.

root slanting anteriorly from the crown and somewhat compressed, as is usual in the P1 of multituberculates. The posterior root, in contrast, is broad transversely. The crown has three main conical cusps arranged in a triangle. Two of the cusps are aligned mesiodistally on the lingual side of the tooth, and a small rise is positioned labial to the anterior cusp. This prominence gives a subrectangular aspect to the crown in occlusal view. Details of the labial side are difficult to establish, because part of the enamel has been chipped away in this area.

P3 is also double-rooted, with a slightly posterior inclination. The crown is low and

has four conical cusps arranged in two mesiodistal rows of two cusps each. Those of the lingual row are higher than the labial cusps.

P4 has two long, lateromedially compressed roots. The narrow, elongate crown is dominated by a row of five cusps that run along the anteroposterior axis of the lingual half of the crown. The third cusp in this row, occupying a central position in the crown, is the most robust. Labial to the three anteriormost cusps in this row are two cusps that form a partial second row. Both are very small and indistinct, especially the posterior one. A broad wear facet extends lingually from the principal row of cusps in the posterolingual portion of the tooth. It is probable that one or more small, lingual cusps occupying this position have been worn away. As in other multituberculates, the main row of cusps of P4 is continuous with the outer row of cusps in M1.

MOLARS: There are two molars in *Tombaatar*; those of the left side have been less exposed to weathering and are better preserved. The cusps in both molars are subhexagonal and very broad; no crescent cusps are present. M1 has a long, compressed, anterior root (the only one exposed), and a cusp formula of 4-5-2. In the labial row, the cusps become slightly larger from the first to the third, the fourth being smaller than the third. A conspicuous crest links the second and third cusp of the labial row, and consequently, there is almost no embrasure between these cusps, a condition not occurring elsewhere in the dentition. Cusp size increases posteriorly in the middle row, from the first to the fourth cusp, the largest of the tooth. The fifth is much smaller than the fourth and subequal to the second of the same row. The cusps of the lingual row form a distinctive lobe, extended from the level of the embrasure of cusps 3-4 of the middle row to the posterior margin of the tooth. The valleys between cusps are very narrow and angular due to the intercalation of the cusps of the central and labial rows, and the roughly hexagonal bases of the cusps.

M2 is double-rooted with two stout, procumbent, and columnar roots. The crown faces anteroventrally; this attribute, together with the ventral projection of the premaxilla,

confers (in lateral view) the characteristic concave outline of multituberculate dentition. The crown has a labial ridge and two more lingual rows with the cusp formula 2-3. The labial ridge is slender and moderately constricted at the level of the anterior cusp of the central row, without forming independent cusps. The two cusps in the middle row are very large, especially the first one that occupys an almost central position. The three lingual cusps are subequal, relatively acute, and tall.

DISCUSSION

Comments on *Djadochtatherium*

In the course of study of *Tombaatar*, the referred specimen of *Djadochtatherium* (AMNH 21703) was further prepared and some new features were exposed. Although this specimen was assigned to *Djadochtatherium* by Gregory and Simpson (1926), it is not, in our opinion, congeneric with the type of *Djadochtatherium matthewi* (AMNH 20440), supporting earlier doubts raised by Kielan-Jaworowska (1970: 45). The maxilla in the referred specimen is representative of an adult specimen, because P1, the last replaced premolar in multituberculates (GWR personal obs.), is freshly erupted while P2 already shows evidence of extensive wear. The maxilla and the premolars are, however, too small to pertain to *Djadochtatherium*. Additionally, the referred and type specimen differ in the shape and size of the anterior zygomatic crest (Gambaryan and Kielan-Jaworowska, 1995), which is low, anteriorly tapered, and small in AMNH 21703, while it is very broad and ends abruptly anteriorly in *Djadochtatherium*. *Djadochtatherium* shares the presence of a horizontal shelf, or cheek, forming the floor of the infraorbital canal with *Catopsbaatar* and *Tombaatar*, whereas such a structure is absent in the specimen referred to *Djadochtatherium*. AMNH 21703 has a constriction in front of the root of the zygomatic arch, but in *Djadochtatherium* the arch and the rostrum are confluent. AMNH 21703 could be a new taxon but it is too poorly preserved to warrant a name. It is considered here as an indeterminate multi-tuberculate which resembles *Nemegtbaatar*, but is larger.

Comments on *Tugrigbaatar saichanensis*

Kielan-Jaworowska and Dashzeveg (1978) reported on a new taxon from the Upper Cretaceous locality, Tugrugeen Shireh, Mongolia. The type and only known specimen of this taxon, *Tugrigbaatar saichanensis*, is an incomplete skull and lower jaw with associated partial humerus and ulna. Kielan-Jaworowska and Dashzeveg compared *Tugrigbaatar* directly with *Kryptobaatar* because of their obvious similarities and discussed a number of differences between them. According to these authors, the most substantial difference between the two genera is the structure of the basioccipital (Kielan-Jaworowska and Dashzeveg, 1978), namely the presence of a basioccipital box in *Kryptobaatar* which is absent in *Tugrigbaatar*. This structure in *Kryptobaatar* later proved to be an artifact (Kielan-Jaworowska et al., 1986). Direct comparison of the specimens reveals that other purported distinctions, such as the different proportions of the premaxillae, glenoid, squamosal portion of the zygomatic arch and tooth size, do not appear to be substantially different from those of some other *Kryptobaatar* specimens. The foramina in the premaxilla present in *Tugrigbaatar* are, however, not found in any of the specimens of *Kryptobaatar* available to us. The peculiar shape of the skull of *Tugrigbaatar* in lateral view, particularly the proportionally inflated nasal cavity (Kielan-Jaworowska and Dashzeveg, 1978:fig. 2), is a consequence of the fact that the back part of the skull roof is missing, and the reconstruction has not been corrected to reflect the missing bone.

The slightly larger tooth and skull sizes of *Kryptobaatar* specimens from Tugrugeen Shireh (PSS-MAE 113, for example) relative to those from Bayn Dzak and Uhkaa Tolgod, and the foramina in the premaxilla in the type specimen of *Tugrigbaatar*, do not provide enough basis for recognition of a distinct genus. Consequently, we propose to make *Tugrigbaatar* a junior synonym of *Kryptobaatar*. The status of the species is in our opinion uncertain with the material available. Kielan-Jaworowska et al. (in press) also

raise doubts about the validity of *Tugrigbaa-tar saichanensis* and consider it to be a valid species of *Kryptobaatar*.

Cladistic Analysis

Several recent studies of multituberculate relationships (cf. Rowe, 1988, 1993; Wible and Hopson, 1993; Wible et al., 1995; Meng and Wyss, 1995; Sereno and McKenna, 1995; Rougier et al., 1996) either lack a comprehensive analysis of interrelationships among multituberculate groups or offer only an analysis of a subset of taxa (Simmons and Miao, 1986; Stevens, 1988; Hahn, 1993). Simmons' (1993) study is the only cladistic analysis available that includes a comprehensive attempt to resolve the relationships of most multituberculate groups. Accordingly, Simmons' (1993) matrix and taxa were used to establish the relationships of *Tombaatar* through the use of PAUP and the assumptions and procedure outlined under Material and Methods.

This preliminary assessment is focused on the placement of *Tombaatar*. It does not presume to be a review of all the characters and coding proposed by Simmons (1993). Only the coding of *Catopsbaatar*, *Nemegtbaatar*, *Djadochtatherium*, and *Kryptobaatar* have been fully inspected. A revision of the taxa and characters in this matrix is in progress as part of larger project on multituberculate phylogeny. The changes are justified below following the character numeration of Simmons, 1993, given here in appendix 1:

9) p4 cusp count: The coding for *Djadochtatherium* is changed from 0 to ?. p4 of the type is now lost, and due to its poor preservation, Simpson (1925) was unable to describe any feature of the occlusal portion of the premolar.

13) m1 cusp formula: *Djadochtatherium*, change from 1 to ?. The preservation of the molars is insufficient to warrant the coding of this character, especially when one more cusp, or less, can change the character state for the taxon.

16) m2 length: *Djadochtatherium* is changed from ? to 1. Although m2 is unknown for *Djadochtatherium*, the distance between the alveoli for the anterior and posterior root is 3.7 mm. This falls in the middle

of the interval 3.0–4.4 mm, which is assigned the condition 1.

17) Central basin on m2: The coding for *Djadochtatherium* is changed from 1 to ?. As stated above, m2 is not known for this taxon.

19) Number of cusps of I2: *Catopsbaatar* is changed from ? to 1. Fewer than four cusps, probably a single cusp, is characteristic of *Catopsbaatar*.

20) Enamel covering of the I2: *Kryptobaatar* is changed from 0 to 1. The enamel is thicker on the labial side of the incisor than on the lingual side (state 1) in the specimen PSS-MAE 113.

21) Number of cusps of I3: *Djadochtatherium* and *Catopsbaatar* are changed from 0 to ?. In both taxa they are broken or heavily worn.

28) P1 cusp count: *Catopsbaatar* is changed from 1 to ? . According to Kielan-Jaworowska (1974), the number of cusps in P1 is not known for this taxon.

33) P3 cusp formula: *Djadochtatherium* and *Catopsbaatar* are changed from 1 to ?. The crown features of P3 are unknown in these multituberculates.

44) Position of aperture of infraorbital canal: The coding for *Djadochtatherium* is changed from ? to 1. In the very incomplete rostrum of the type, the infraorbital canal is not very well preserved, but the position of the anterior aperture can be established with confidence.

46) Length of facial process of maxilla (measured from root of zygomatic process): *Kryptobaatar* is changed from 1 to 0. The skulls PSS-MAE 101 and PSS-MAE 113 of *Kryptobaatar* show the primitive condition.

47) Bony roof over anterior orbital space: *Djadochtatherium* is changed from 0 to 1. The miscoding of this trait stems from Simpsons (1925) restoration of the skull. What he interpreted as the orbit is actually a missing portion of the lateral wall of the nasal cavity. Fragments of the maxilla and probably lacrimal are missing from this sector of the skull. The orbit in fact is placed more posteriorly and only the most anterior wall of it is preserved in *Djadochtatherium*. A distinct suture between the maxilla and another element, probably the lacrimal, is visible in the orbit. What is preserved of this anterior wall of the orbit inclines posteriorly, as in other

multituberculates in which there is a bony roof over the anterior part of the orbit.

48) Snout confluent with zygomatic arch: *Nemegtbaatar* is changed from 1 to 0. In our opinion, the rostrum is not confluent with the zygoma.

50) Zygomatic ridge: *Catopsbaatar* is changed from 0 to 1. The zygomatic ridge is well developed in *Catopsbaatar* (Gambaryan and Kielan-Jaworowska, 1995).

51) Size of postorbital process: *Kryptobaatar* and *Catopsbaatar* are changed from 0 to 1. The postorbital process is large in *Kryptobaatar* (PSS-MAE 113); previous reports of small processes (Kielan-Jaworowska, 1974; Kielan-Jaworowska and Dashzeveg, 1978) were based on incomplete material. *Catopsbaatar* also has very large postorbital processes (Kielan-Jaworowska, 1974, plate XIX, 1c).

53) Shape of frontoparietal suture: *Djadochtatherium* is changed from 0 to ?, and *Kryptobaatar*, from 0 to 1. The posterior portion of the frontals is not present in the type of *Djadochtatherium* and the suture is distinctively U-shaped in *Kryptobaatar* (PSS-MAE 113).

54) Contact between nasals and parietals: *Djadochtatherium* is changed from 1 to ?, and *Kryptobaatar*, from ? to 0. The miscoding of this feature probably follows Simpsons (1925) restoration of the parietal contact with the nasals. No such contact is present in the type. In *Kryptobaatar* the parietal does not reach forward beyond the middle point of the orbit, and thus it does not approach the nasals.

55) Lacrimal size: *Kryptobaatar* is changed from ? to 0 and *Catopsbaatar* from 0 to 1. The problem with the condition in *Djadochtatherium* is again related to the original interpretation of the orbit by Simpson (1925), which Simmons followed in her analysis. In fact, the missing bone in the lateral wall of the nasal chamber may have been mostly lacrimal. The rostral extension of the lacrimal in *Djadochtatherium* cannot be determined precisely with the specimen available, but enough remains to establish that the facial process was extensive, similar to the condition of other Mongolian multituberculates, which are coded as 1.

56) Thickenings in palatal process of the premaxilla: *Djadochtatherium* and *Catopsbaatar* are changed from 0 to 1. In *Djadochtatherium*, a distinct, elongated prominence is present on the left premaxilla of the type, occupying the same position as in other multituberculates with a thickened premaxilla. The thickening is also present in *Catopsbaatar* (ZPAL-MgM I/79).

58) Palatal vacuities: *Djadochtatherium* and *Kryptobaatar* are changed from 1 to ? and 0, respectively. The preservation of the palate in *Djadochtatherium* does not warrant the recognition of palatal vacuities; the type even suggests that the vacuities were absent. Until better skulls are available, a decision on this matter seems premature. Specimens better preserved than the type of *Kryptobaatar* (Kielan-Jaworowska. 1970) available to Kielan-Jaworowska and Dashzeveg (1978) show that the previously reported palatal vacuities in this taxon are artifacts. This is confirmed by our specimens.

59) Position of posterior border of palate with regard to M2: *Nemegtbaatar* and *Catopsbaatar* are changed from 1 to 2. In both, the palate extends posteriorly up to the embrasure between M1 and M2 (Kielan-Jaworowska, 1974; Kielan-Jaworowska et al., 1986).

60) Ethmoid foramen present: *Kryptobaatar* is changed from ? to 0. The foramen is present in the skulls collected by the new Mongolian-American Museum Expeditions (PSS-MAE 101 and 113).

64) Position of the internal carotid foramen; 65) presence of condylar foramina; and 66) number of condylar foramina: *Kryptobaatar* is changed from ? to 1 based on the new specimens.

PAUP Results

Only heuristic searches were conducted because of the large amount of missing data and the high number of taxa. The number of trees produced, even after the deletion of the taxa considered to be taxonomically equivalent (Wilkinson, 1995), was so large that none of the searches were completed. After some runs, the MAXTREES option of PAUP was set at 20,000, which approximates the maximum number of trees that could be stored in memory by the available computer.

The topology of the consensus of the 20,000 does not differ from the topology of the consensus of 10,000, the latter being the number of trees considered in Simmons (1993) study.

Comparison of the strict consensus tree (fig. 6A) to the tree presented by Simmons (1993) reveals that the changes introduced in the coding and the additional taxa decreased resolution. Despite the numerous trees and the insensitivity of the strict consensus methods for recovering recurrent structure among the most parsimonious trees (Mickevich and Platnick, 1989; Funk and Brooks, 1990), a fair number of nodes are still present in the strict consensus tree (fig. 6A). Recent advances in our knowledge of multituberculates justify a revision of the taxa and characters included in the matrix presented here (appendix 2), but that is beyond the scope of this paper. Accordingly, only a few major issues emerging from the results of this study are considered.

Relationships of *Tombaatar*

A monophyletic assemblage formed by *Tombaatar, Catopsbaatar, Djadochtatherium, Nemegtbaatar, Bulganbaatar, Kryptobaatar*, and *Chulsanbaatar* as successive sister groups is recovered in the consensus tree (fig 6A, node 3). This arrangement for *Catopsbaatar* and *Djadochtatherium* is similar in some regards to the traditional view (e.g., Clemens and Kielan-Jaworowska, 1979; Hahn and Hahn, 1983) that these taxa are closely related. Instead, Simmons (1993) proposed a closer relationship of *Djadochtatherium* with taeniolabidids than with any other Late Cretaceous multituberculate from Mongolia. She remarked, however, that the position of *Djadochtatherium* (forming a monophyletic group with the Taeniolabidoidea) was one of the weakest supported nodes in her cladogram. The relationships proposed here for *Tombaatar* contradict Simmons arrangement in that *Djadochtatherium, Catopsbaatar*, and the new taxon are not closely related to Taeniolabididae, but form a group outside ptilodontoids and taeniolabidoids (all multituberculates more closely related to Taeniolabididae than to Ptilodontidae). The tree topology of Simmons study is five steps longer than the consensus tree presented

here. In general, our study recognizes *Tombaatar* as another lineage of the diverse monophyletic clade of mostly Asiatic multituberculates (fig. 6A, node 1). These Late Cretaceous multituberculates show a general increase in body size, a reduction of the anterior premolar elements and, in the most specialized cases, a loss of P2 (Kielan-Jaworowska, 1974; Clemens and Kielan-Jaworowska, 1979), features apparently acquired convergently with those in Taeniolabididae, as also implied by Simmons' (1993) cladogram.

A monophyletic assemblage of the Late Cretaceous multituberculates from the Djadokhta and Barun Goyot Formations, in addition to *Pentacosmodon* (Jepsen, 1940) from the Paleocene of North America, is supported by the 50% majority rule consensus tree (fig. 6C) as well as cladograms based on successively more complete taxa (e.g., 30% or more complete, 35%, 45%), although the internal structure of the basal members of this clade is left unresolved in the strict consensus tree. This primarily Mongolian group consistently falls outside the monophyletic assemblage comprising ptilodontoids and taeniolabidoids. This conclusion does not contradict Simmons' (1993) tree, because her group X (including most of the Late Cretaceous multituberculates and *Pentacosmodon*) was included in a polytomy involving ptilodontids, taeniolabidoids, *Sloanbaatar, Bulganbaatar, Hainina*, and *Paracimexomys*. Nonetheless, Simmons applied the name Cimolodonta (McKenna, 1975; Stucky and McKenna, 1993) to this node and redefined the group as the last common ancestor of *Ptilodus* and *Taeniolabis* plus all its descendants. The resolution of that polytomy in the tree herein indicates that the Late Cretaceous multituberculates from Mongolia should not be considered cimolodonts sensu Simmons (1993). Eucosmodontidae is also inappropriate for this clade of mostly Mongolian multituberculates, because applying the traditional concept of membership (Clemens and Kielan-Jaworowska, 1979; Hahn and Hahn, 1983) renders the group paraphyletic (Stevens, 1988; Simmons, 1993). Hence, a new name for this group is warranted, pending a more complete review of the data set employed here. In recognition of our current un-

certainty about the relationships of the multituberculates from the Late Cretaceous of Mongolia, we refer *Tombaatar* and its relatives to a family incertae sedis.

As in Simmons' (1993) tree, the core of both Ptilodontoidea and Taeniolabidoidea is also recovered in this analysis (fig. 6), but, as mentioned above, these groups form a monophyletic assemblage excluding the Asiatic Late Cretaceous multituberculates, with the possible exception of *Buginbaatar* (Kielan-Jaworowska and Sochava, 1969). The age of *Buginbaatar* is somewhat uncertain; it could be either Late Cretaceous or Paleocene (Clemens and Kielan-Jaworowska, 1979). Jerzykiewicz and Russell (1991), however, correlated the strata bearing *Buginbaatar* (Khaichin Ula, in the Bugin Cav region) with those of the Nemegt Formation. If so, *Buginbaatar* would be the only known mammal of the Nemegt Formation representing a younger interval than that represented by the Djadokhta and Barun Goyot Formations. Consequently, no other mammalian taxa can be utilized to establish whether the Gobi mammalian fauna during

"Nemegt times" was basically endemic or closely linked with faunas from other continents. A greater affinity between multituberculate faunas of North America and Asia is seen in the case of late Paleocene multituberculates such as *Catopsalis* (Sloan and Kielan-Jaworowska, 1979; Simmons and Miao, 1986), *Sphenopsalis* (Matthew et al., 1928), *Prionessus* (Matthew and Granger, 1925; Matthew et al., 1928) and *Lambdopsalis* (Chow and Qi, 1978; Miao, 1988).

Additional important differences between our tree and that of Simmons (1993) are the collapse of her node Y of taeniolabidoids into a series of paraphyletic groups and individual taxa; the removal of *Cimolodon* from Ptilodontoidea to Eucosmodontidae (at least in the 50% majority rule consensus); and the transfer of *Cimolomys* from Simmons' group Z to a basal position in Taeniolabidoidea.

Noteworthy is the distinctiveness of some of the mammals from the new locality, Ukhaa Tolgod (Novacek et al., 1994; Dashzeveg et al., 1995), which includes several as yet undescribed taxa of multituberculates and
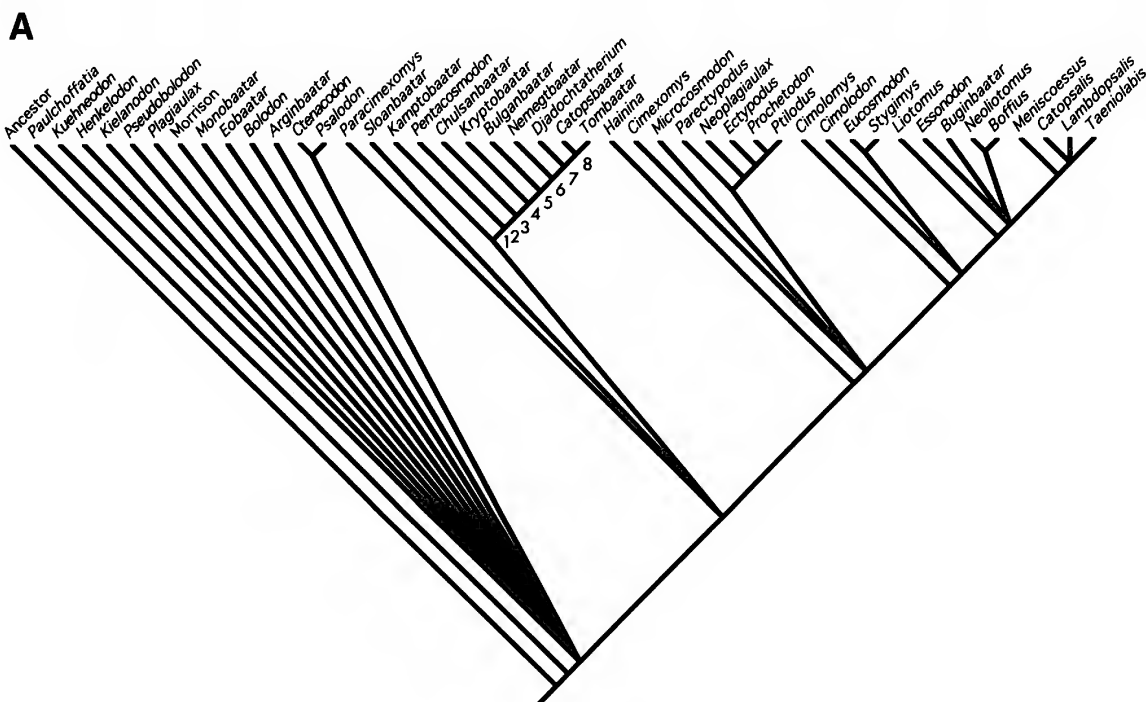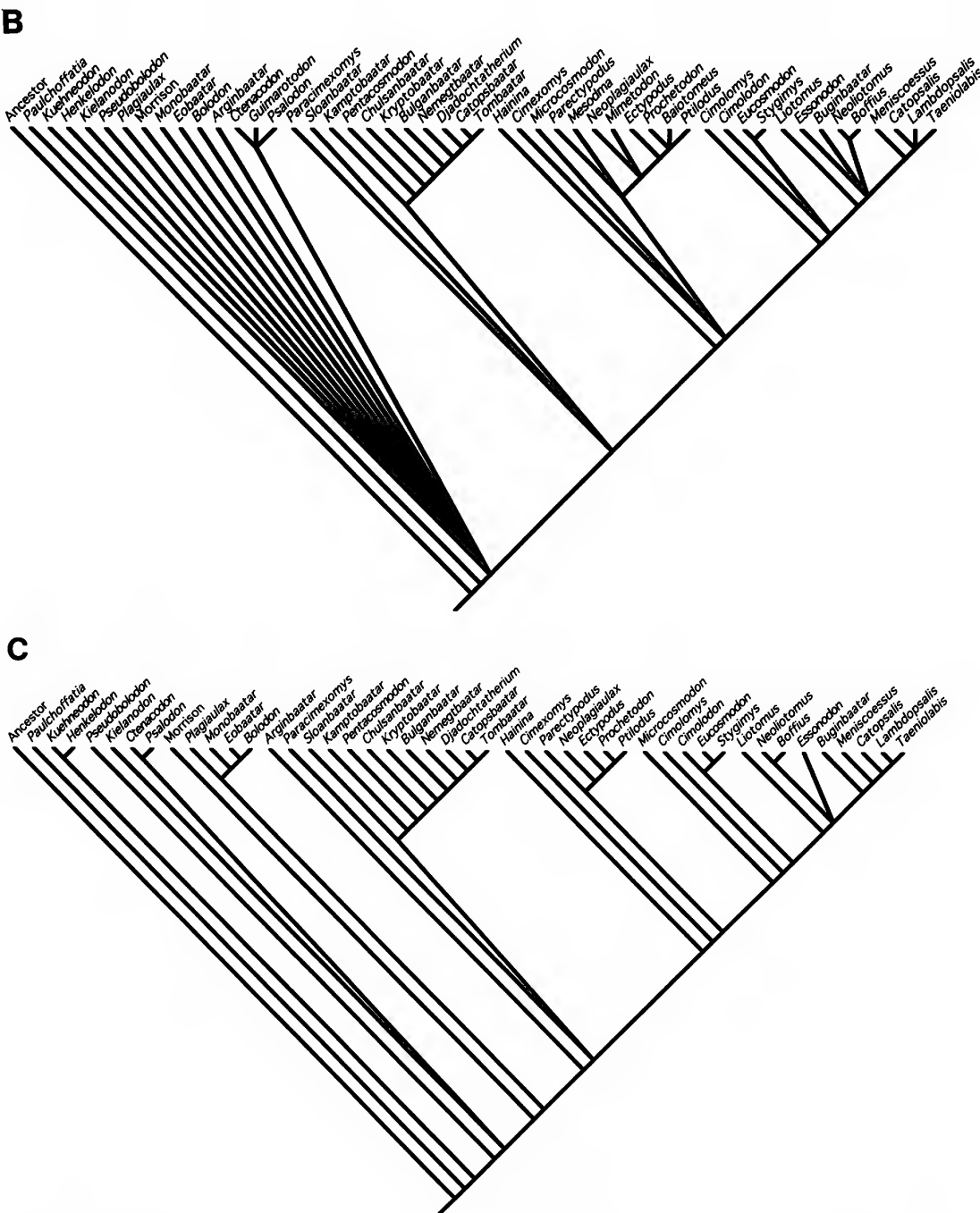

Fig. 6.

Fig. 6. *Continued.* (A) Strict consensus tree of 20,000 equally most parsimonious trees produced by heuristic search by PAUP. Four taxa scored in the matrix, *Guimarotodon, Mesodma, Mimetodon,* and *Baiotomeus,* have been considered TET and omitted. The strict consensus tree has the following parameters: tree length = 284; CI = 0.38 and the RI = 0.652. The same parameters for the individual trees are tree length = 242; CI = 0.446; RI = 0.735. Numbers relate to the nodes diagnosed in appendix 3. (B) Strict consensus tree of 20,000 most parsimonious trees with the TET added. (C) 50% majority rule of the 20,000 equally most parsimonious trees. This tree, with minor differences, is also recovered in the strict consensus of trees that considered successively more complete taxa (30%, 35%, 40%, 45% and 50% or more complete).

therians in addition to *Tombaatar*. In a more general framework, the similarities between the Late Cretaceous mammals from Mongolia and those from other continents are very vague, especially in light of the unsettled status of the higher-level systematics of Multituberculata and the uncertain affinities of *Asioryctes* and *Kennalestes* (Novacek, 1986; MacPhee and Novacek, 1993). All mammalian genera from the Late Cretaceous of Mongolia are endemic forms. No member of Zalambdalestidae (Gregory and Simpson, 1926; Nessov and Kielan-Jaworowska, 1991; Averianov and Nessov, 1995), or of the various multituberculate families recognized by Kielan-Jaworowska (1971, 1974), is known outside Mongolia and the former Soviet Mid-Asia. Deltatheridiidae are possibly represented in North America by isolated molars (Fox, 1974; Cifelli, 1990), but the ptilodontoids, abundant in North America, are altogether absent from Mongolia (Kielan-Jaworowska, 1975, 1980; Kielan-Jaworowska and Sloan, 1979; Bonaparte and Kielan-Jaworowska, 1987).

To sum up, this preliminary analysis suggests that most or all of the Late Cretaceous multituberculates from Mongolia form an indigenous group without close relationships with those from other continents. *Pentacosmodon* from the Paleocene of North America may be a later branch of that Mongolian group. This group could be the sister group of Cimolodonta (ptilodontoids + taeniolabidoids). The presence of other endemic Mongolian mammals makes this scenario possible but its definitive test will be provided by a comprehensive revision of multituberculate relationships in progress.

The infraorbital canal and nasal cavity in multituberculates

The presence of multiple exits of the infraorbital foramen in non-mammalian Mammaliamorpha and basal mammals is well documented (Kermack et al., 1981; Hahn, 1985; Rowe, 1988, 1993; Lillegraven and Krusat, 1991; Rougier, 1993). Following remarks by Kemp (1983) and Hahn (1985), characters of the infraorbital canal, including number, size, and relationships of the apertures have been included in different phylogenetic studies (Rowe, 1988, 1993; Wible, 1991; Rougier, 1993). The importance of the distinction of the number of exits for the branches of the maxillary branch of the trigeminal nerve and accompanying vascular structures has been questioned by Miao (1988). The discrepancies cited by Miao have, however, no bearing in a major phylogenetic framework, because the variation he noted occurs in only a few very disparate groups. The infraorbital canal transmits the major vessels and nerves that supply the rostrum, including the lips and rhinarium, which are both characteristic mammalian features. For that reason, further analysis of the canal and associated structures is warranted.

All the Late Cretaceous multituberculates from Mongolia have a single aperture for the infraorbital canal, supposedly foramen 1 (Hahn, 1985). Hurum (1994), in his study of the multituberculate rostrum using transverse sections, observed that in the available specimens the infraorbital canal was open medially into the nasal cavity. He cautioned, however, that this condition could be caused by defects of preservation. The same precautions are needed in evaluating *Tombaatar*, whose maxilla has the infraorbital canal confluent with the nasal cavity, although the whole area is badly preserved. The infraorbital canal is confluent with the nasal cavity in non-mammaliamorph synapsids (Kemp, 1982, 1983) and also in the docodont *Haldanodon* (Lillegraven and Krusat, 1991), but it is separated in a closed canal in tritylodontids (Kühne, 1956) and *Morganucodon* (Kermack et al., 1981). However, other Cretaceous multituberculates from Mongolia have the infraorbital canal completely separated from the nasal cavity, as in *Kryptobaatar* (PSS-MAE-113) and the specimen originally attributed to *Djadochtatherium* (AMNH 21703). Consequently, regardless of the primitive condition for this character in Multituberculata, the separation of the infraorbital canal from the nasal cavity seems to be a homoplastic trait in mammaliamorphs.

One foramen in the fragmentary maxilla AMNH 21703 (the specimen originally referred to *Djadochtatherium*) and two foramina in *Kryptobaatar* (PSS-MAE 113) pierce the medial wall of the infraorbital canal to communicate either with the nasal cavity or

the maxillary sinus. In AMNH 21703, the single aperture is quite large and opens very close to the posterior aperture of the infraorbital canal. Additional preparation of the specimen shows that this foramen penetrates the substance of the maxilla. It may connect with a maxillary sinus, which does not communicate, at least in the portion preserved, with the nasal cavity. The two medial apertures of the infraorbital canal in *Kryptobaatar* probably have a similar relationship with respect to the maxillary sinus. The presence of maxillary sinuses seems to be a widespread feature among the multituberculates from the Late Cretaceous of Mongolia, being present not only in *Chulsanbaatar*, *Nemegtbaatar*, and *Tombaatar* (Hurum, 1994; this study), but also in many unidentified skulls in which portions of the nasal cavity are exposed. Maxillary sinuses are absent in monotremes and *Didelphis* and are variably developed among placentals (Paulli, 1900; Moore, 1981; Novacek, 1993). In some living mammals, as in *Canis* (Evans and Christensen, 1979), small foramina open inside the infraorbital canal. They lead through the alveolar canals to the apex of each alveolus and transmit branches of the V_2 and blood supply. It is possible that some of the small foramina in the infraorbital canal of multituberculates can be explained as the apertures of the alveolar canals.

We emphatically agree with Simpson's (1937) remark that the nasal bone in multituberculates was extraordinarily developed. The nasal cavity of multituberculates, especially those from the Late Cretaceous from Mongolia, is very large when compared to those of most living mammals. In fact, the so-called sphenoidal sinuses in *Nemegtbaatar* and *Chulsanbaatar* (Kielan-Jaworowska et al., 1986; Hurum, 1994) lack a septum separating them from the nasal cavity; they are continuous in the transverse sections shown by those authors. Fragments of bone are preserved inside the cavity; but these do not allow distinction of any kind of separation between the nasal cavity and each sphenoidal sinus. The fragments illustrated can be equally explained as parts of turbinals or remnants of a septum. Considering the enormous size of the anterior portion of the nasal cavity and associated paranasal sinus system,

in addition to the dorsal position of the frontal lobes (Kielan-Jaworowska, 1983, 1986), it is possible that the so-called sphenoidal sinus of multituberculates is, in fact, a posterior expansion of the nasal cavity. This agrees with the consistently large olfactory bulbs of available multituberculate endocasts (Simpson, 1937; Kielan-Jaworowska, 1983, 1986; Krause and Kielan-Jaworowska, 1993).

Tombaatar and the new specimens of *Kryptobaatar* available to us support Miao's (1988) claim that the absence of an orbital process of the palatine can be considered synapomorphic for those Multituberculata in which this area of the skull is known (i.e., cimolodonts plus Mongolian multituberculates). Hurum (1994) has recently disputed this idea based on a serially sectioned skull of *Nemegtbaatar* purportedly showing an orbital process of the palatine. However, the sections illustrated are ambiguous, and the bone in that sector might be maxilla, as in comparable sections of *Chulsanbaatar* (cf. fig. 9 and 16 of Hurum, 1994).

ACKNOWLEDGMENTS

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TABLE 1

Measurements of Premolars and Molars of Tombaatar (mm)

	Left			Right		
	Length	Max. width	Min. Width	Length	Max. width	Min. width
P1	1.45	1.61	?	?	?	?
P3	1.92	1.41	?	?	?	?
P4	3.73	1.69	?	3.52*	1.50*	?
M1	5.46	3.35	2.43	5.51	3.24	2.40*
M2	3.7	3.53	?	3.75	3.48	?

* Estimated measurement.

Appendix 1

Character List

Dental characters

1. Enamel ultrastructure preprismatic (0), gigantoprismatic (1), or small prismatic (2). Unordered.
2. Root of lower incisors does not extend posteriorly under p3 and p4 (0), or does extend under p3 and p4 (1).
3. Enamel covering of lower incisor of uniform thickness (0), thicker on labial surface than on lingual surface (1), or completely restricted to labial surface of tooth (2). Ordered.
4. Lower incisor not laterally compressed (0), or laterally compressed (1).
5. p1 present (0), or absent (1).
6. p2 present (0), or absent (1).
7. p3 present (0), or absent (1).
8. p3 cusp count 3–5 (0), or 1–2 (1).
9. p4 cusp count 3–4 (0), 5–7 (1), 8–10 (2), or 11–15 (3). Ordered.
10. p4 length 1.0–2.4 mm (0), 2.5–5.2 mm (1),

5.3–7.4 mm (2), or 7.5–15.0 mm (3). Ordered.

11. p4 in lateral view has straight anterior (leading) edge set at sharp angle to crown (0), or has arcuate leading edge blending into arcuate crown (1).
12. p4 diphyodont (0), or monophyodont (1).
13. m1 cusp formula 4:3 or lower (0), 4:4 (1), 5:4 (2), or 7:4 or higher (3). Ordered.
14. m1 length 1.0–2.9 mm (0), 3.0–5.4 mm (1), 5.5–6.4 mm (2), 6.5–10.9 mm (3), 11.0–22.0 mm (4). Ordered.
15. m2 cusp formula 0:1 (0), or 2:2 or more (1).
16. m2 length 1.0–2.9 mm (0), 3.0–4.4 mm (1), 4.5–9.9 mm (2), 10.0–17.0 mm (3). Ordered.
17. m2 with central basin present (0), or absent (1).
18. I1 present (0), or absent (1).
19. I2 cusp count 4 (0), or 3 or fewer (1).
20. Enamel covering of I2 of uniform thickness (0), thicker on labial surface than on lingual surface (1), or completely restricted to labial surface of tooth (2). Ordered.
21. I3 with multiple cusps (0), or single cusp (1).

22. I3 located on margin of palate (0), or in medial position near sagittal midline (1).
23. Canine present in upper dentition (0), or absent (1).
24. Canine cusp count 4 (0), or 3 or fewer (1).
25. P0 present (0), or absent (1).
26. P0 cusp count 4 (0), or 2–3 (1).
27. P1 present (0), or absent (1).
28. P1 cusp count 4 (0), or 3 (1).
29. P2 present (0), or absent (1).
30. P2 cusp count 5–6 (0), 4 (1), or 3(2). Ordered.
31. P2 double-rooted (0), or single-rooted (1).
32. P3 present (0), or absent (1).
33. P3 cusp formula 1:2 (0), 2:2 (1), 2:4 (2), or 3:4 (3). Ordered.
34. P3 double-rooted (0), or single-rooted (1).
35. P4 cusp formula 0–5; 1–4; 0–5 (0); 0–5:5–10:0–5 (1), or 0–5:5–10:8–12(2). Ordered.
36. P4 length 0.5–3.4 mm (0), 3.5–5.4 mm (1), 5.5–8.4 mm (2), or 8.5–11.0 mm (3). Ordered.
37. P4 double-rooted (0), or single-rooted (1).
38. M1 cusp formula 2–3:2–4:0 (0), 4–5:4–5:0–1 (1), 5–7:5–8:2–5 (2), or 5–11:7–10:6–11 (3). Ordered.
39. M1 length 1.0–3.9 mm (0), 4.0–5.9 mm (1), 6.0–7.9 mm (2), 8.0–11.9 mm (3), or 12.0–25.0 mm (4). Ordered.
40. M2 lingual cusp row absent (0), or present (1).
41. M2 length 0.5–3.9 mm (0), 4.0–5.4 mm (1), 5.5–8.9 mm (2), or 9.0–17.0 mm (3). Ordered.

Cranial characters

42. Premaxilla with facial process height > anteroposterior length (0), or height ≤ length (1).
43. Number of infraorbital foramen foramina, 2 (0), or 1(1).
44. Primary infraorbital foramen (FiI sensu Hahn, 1985) opens anteriorly and laterally on face, not visible in ventral view (0), or opens ventrally (1).
45. Primary infraorbital foramen (FiI sensu Hahn, 1985) positioned dorsal to P1 (0), dorsal to P2 (1), or dorsal to P3 or P4 (2). Ordered.
46. Maxilla with facial process length (measured from posterior edge of base of zygomatic arch) > height (measured from same point) (0), or length < height (1).

47. Bony roof over anterior orbital space absent (0), or present (1).
48. Flare present in zygomatic arch, snout not confluent with zygomatic arch (0), or flare absent, snout confluent with zygomatic arch (1).
49. Base of zygomatic arch (as marked by posterior edge) directly dorsal or anterior to P3/P4 embrasure (0), dorsal to P4 (1), or dorsal or posterior to P4/M1 embrasure (2). Ordered.
50. Zygomatic ridge absent or very faint (0), or strongly developed (1).
51. Postorbital process absent or very small (0), or large (1).
52. Snout length < 45% of total skull length (0), or > 50% of skull length (1).
53. Frontal-parietal suture V-shaped (0), or U-shaped (1).
54. Contact between nasals and parietals absent (0), or present (1).
55. Lacrimal large, extends anteriorly as far as frontals do (0), small, does not extend as far as frontals (1), or absent from face (2). Unordered.
56. Thickenings in palatal process of premaxilla absent (0), or present (1).
57. Incisive foramina small, round to oval (0), medium size, elongate (1), or very large with palatal fossae (2). Unordered.
58. Palatal vacuities absent (0), or present (1).
59. Posterior border of palate medial or posterior to posterior edge of M2 (0), medial to middle of M2 (1), or medial to M1/M2 embrasure (2). Ordered.
60. Ethmoid foramen present (0), or absent (1).
61. Foramen masticatorium (or subdivisions of same) lateral and slightly anterior to foramen ovale inferium (0), or anterior and slightly medial to foramen ovale inferium (1).
62. Jugular fossa small and shallow (0), or large and deep (1).
63. Sulcus medialis present (0), or absent (1).
64. Internal carotid foramen pierces basisphenoid, carotid canal enters pituitary fossa from below (0), or foramen opens at junction of basisphenoid, petrosal, alisphenoid, and pterygoid; carotid canal enters pituitary fossa laterally (1).
65. Condylar foramina present (0), or absent (1).
66. Condylar foramina paired (0), or single (1).
67. Angle of coronoid process relative to tooth row, steep, > 55 degrees (0), or low, < 45 degrees (1).

Appendix 2

Taxon-Character Matrix

Character number	111111111122222222223333333333444444444455555555556666666	%
	1234567890123456789012345678901234567890123456789012345678901234567	Compl

Taxon		
Ancestor	?000000??000?0?0?0?0?00?0?0?0?0?00?0?00?0?0?00?000?00000000?00?0000?0	67.2
Paulchoffatia	00000000000?000000?000000000??00100000000000000000??10??0??0??000	80.6
Kuehneodon	0100?000000000000?001?001?00000??000000?0?00010000?????0?0??0?0??0	70.2
Henkelodon	?10010???0?0?0?0??00101?1?0000001000010000???1????????????????????0	19.4
Kielanodon	?????????????????????????????0020000??????????000???????????????	14.9
Guimarotodon	?1000000100?00???	17.9
Pseudobolodon	?100000A?0???0?0?000?001010002002000?????0000?010??????????0?00???	58.2
Ctenacodon	?1000000100?00??1?????1?010102000300001000?001?00??????????????0	55.2
Psalodon	?100000?110?00??000001?010102000300??????????????????????????	44.8
Plagiaulax	?1001000210?00??1???0	20.9
Morrison	11210000100?001010121001010102002000010100000110200?0000000A??????0	86.6
Monobaatar	?????????????????????01010200300???10?101?000??????????????	29.9
Eobaatar	11201000210?00101??????0101010030000010?????????????????????????0	50.8
Bolodon	?????????????????0??1?011?0101003000000??01?110?0???????????????	64.2
Arginbaatar	11001001310?00??1?????0A0101020000000??00?001??010??????????????	44.8
Paracimexomys	1??0????211?A0101???????????????????1010??????????????????????	16.4
Hainina	1???????211?00101?????????01010100B010??????????????????????	34.3
Cimolodon	11001101321?21101?????1?1?01??00101102110?102??010?????????1??????0	58.2
Mesodma	21001101311?B0101?????????????????10020?????0??????????????????	26.9
Parectypodus	21001101311?B0101?????1?1?01020010100201??1020?01?????????????????0	58.2
Ectypodus	21001101311?30101?10??1?1?010100101003010?1020101000002?21211011010	88.1
Mimetodon	2???1101B11?30101?????1?1?????00010030101?1020?01?????????????????0	46.3
Neoplagiaulax	21001101311130101?????1?1?010200101003A10?10200010?????????????0	62.7
Prochetodon	21001101331?30???????1?1?010C002010210110?102?????????????????	47.8
Ptilodus	21001101321?21101110001?1?010100202103010010200010000202121011010	95.5
Baiotomeus	??????0?321?B1101?????????01???020210??????????????????????	37.3
Cimexomys	11101101211?21101?????1?1?010200101002010110210?????????????????0	58.2
Djadochtatherium	?1201101?11??1?1?1???11?1?010200?0??0????11111111?????0?????????0	50.7
Kryptobaatar	11211101211?00101111011?1?0102000100101011101111110010000111110	95.5
Pentacosmodon	11111111?101?00101??	76.1
Chulsanbaatar	?1211101101?001011?0011?1?0102001010010101111101111?011001?11111?0	89.6
Sloanbaatar	?11011??211?00101110011?1?010200101001010111110110110200100011??0	86.6
Kamptobaatar	11101101101?00??11001??1?0102001010010101??11101101102000000?1111?1	86.6
Bulganbaatar	??????????1?????1?1??1?1?010200101002010111111011?????0012????????	49.3
Catopsbaatar	11201101011?12111112?11?1?0?1??0?0110221111111112111011002??1??0	79.0
Nemegtbaatar	11211101111?211011112011?1?0102001010021011111101111100101200111?1	94.0
Microcosmodon	?11111011?1?30101?00????????????A0020????????????????????????0	31.3
Eucosmodon	1121111?B31?21??1?00??????1?0210?11202110?1020?011??????????????1	52.2
Stygimys	1121111?311?31101?00011?1?010210111102110?1011?011??????11??????1	70.2
Liotomus	2???????331?31101?????????010200101?3110??????????????????????	34.3
Neoliotomus	2121110?331?B3??????????????????0??13032???????????????????????	23.9
Boffius	1111???????????????????????????13034??????????????????????	13.4
Essonodon	1???????????33101????????????0?0?003200?????????????1????????	22.4
Cimolomys	1???????211?311??????????????????1002110??????????????????	23.9
Buginbaatar	??????????????????????????????110331??????0?????????????????	11.9
Meniscoessus	11101101221?23121100001?1?010200?0A10331210011?02??????011??????1	70.2
Catopsalis	?120111?01?23121??2?01?1?1?1??1??1133312?????????????????????0	41.8
Lambdopsalis	?120111?00?1231211?2001?1?1?1??1??0013312110?100200101201020?111010	80.6
Taeniolabis	1120111?02?133121?02?01?1?1?1??1??02134120101002001012010???????0	73.1
Tombaatar	??????????????????112?1?1?011??01011110?11011111??0?????001101????????	44.7

Polymorphic characters (uncertainty): A=0&1, B=2&3, C= 1&2

Appendix 3

Diagnoses of Some Relevant Nodes of the Consensus Tree (fig. 6A)

Nodes are diagnosed by listing the derived condition for characters in appendix 1. Multistate characters or reversals are depicted within parentheses following the character number. Asterisks (*) denote equivocal characters. Characters are optimized under an accelerated transformation (ACCTRAN) assumption.

Node 1
9(1) p4 cusp count of 5–7
10(0) p4 length between 1.0 and 2.4 mm
65 Condylar foramina absent
58(0)* Palatal vacuities absent
61* Foramen masticatorium anterior and slightly medial to foramen ovale inferium

Node 2
4 Lower incisor laterally compressed
51* Postorbital process large
55(0)* Lacrimal large, extends anteriorly as far as frontals do
56* Thickening in palatal process of premaxilla present
59(1)* Posterior border of the palate medial to middle of M2

Node 3
3(2) Enamel covering of lower incisors completely restricted to labial surface of tooth

Node 4
10(1) p4 length between 2.5 and 5.2 mm

20(1) Enamel covering of the I2 thicker on labial surface than on lingual surface

Node 5
38(2) M1 cusp formula 5–7:5–8:2–5
59(2) Posterior border of the palate medial to M1/M2 embrasure
13(1)* m1 cusp formula 4:4
14(1)* Mm1 length between 3 and 5.4 mm
58* Palatal vacuities present
61(0)* Foramen masticatorium anterior lateral and slightly anterior to foramen ovale inferium

Node 6
20(2) Enamel covering I2 completely restricted to labial surface of the tooth
39(1) M1 length between 4 and 5.9 mm.

Node 7 (Djadochtatherium, Catopsbaatar, Tombaatar)
4(0) Lower incisor not laterally compressed
16(1) m2 length between 3 and 4.4 mm
48 Flare of the zygomatic arch absent, rostrum confluent with zygomatic arch
9(0)* p4 cusp count of 3–4
36(1)* P4 length between 3.5 and 5.4 mm
58(0)* Palatal vacuities absent

Node 8 (Catopsbaatar + Tombaatar)
29 P2 absent
14(2)* m1 length between 5.5 mm and 6.4 mm

Autapomorphies of Tombaatar
49(0) Base of zygomatic arch (as marked by the posterior edge) directly dorsal or anterior P3/P4 embrasure
57(1) Incisive foramina medium size, elongated
59(1) Posterior border of palate medial to middle of M2